CIRCULATE

VOLUME IX NUMBER 7

MADROÑO

A WEST AMERICAN JOURNAL OF BOTANY

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Published at North Queen Street and McGovern Avenue,
Lancaster, Pennsylvania

July, 1948

MADROÑO

A WEST AMERICAN JOURNAL OF BOTANY

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Entered as second-class matter October 1, 1935, at the post office at Lancaster, Pa., under the act of March 3, 1879.

Established 1916. Published quarterly. Subscription price $3.50 per year. Completed volumes I to VIII $5.00 each; single numbers $1.00.

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Published at North Queen Street and McGovern Avenue, Lancaster, Pennsylvania, for the

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SOME PROBLEMS IN THE GENUS GILIA

Herbert L. Mason and Alva D. Grant

Of all of the genera of Polemoniaceae, the genus *Gilia*, when viewed in terms of the treatments accorded it in the literature of botany, presents the most confused picture. In the first place there has been confusion as to generic limits. With the exception of *Phlox* and *Polemonium* all of the herbaceous genera have at one time or another been included in *Gilia*. The nature of this confusion has been discussed previously by the senior author (1945) and will not be discussed further here. Another aspect of the confusion in *Gilia* results from the fact that the genus is replete with polymorphic species and intergrading populations that seem to defy rational treatment along traditional taxonomic lines. This, it seems to us, relates itself to the nature of the environment and its influence on the genetic elaboration of the populations of species. *Gilia* has its distributional center in the arid southwestern United States. Here, the moisture factor approaches the minimum in several of its aspects and soils display great local and geographic diversity as to origin, maturity, hydrogen ion concentration and degree of leaching of the mineral content. The moisture factor, approaching the minimum as it does, according to Liebig's (1843) law results in striking habitat differences owing to moisture differences of small amount. These local differences result from differences in the annual rainfall or from seasonal fluctuations from year to year in the same area. This latter aspect is of very great significance in the floristic expression in any given desert or semi-arid area from season to season, and appears to manifest itself in a selective way on the threshold of germination of the stored seed that may be present in the soil. One sequence of moisture-temperature variables will cause a given set of seed to germinate while another sequence appears to favor another set. When this fluctuation and geographic variation of the moisture factor is superimposed over the geographic variation in other edaphic conditions there result an enormous number of significant habitats such as one does not encounter in more humid areas. Striking differences in floristics from one habitat to another and from one season to another in the same habitat result. Through their genetic and physiological responses to these varied habitats many genera in many of the families of the arid southwest have become very complex. It is not surprising that the taxonomist working on such genera becomes frustrated in his interpretations unless he has a full appreciation of the potentialities of genetic processes as they function to elaborate the species populations over such habitats. Even then he can utilize this information only in organizing his problem

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Madroño, Vol. 9, No. 6, pp. 169–200. June 9, 1948.

and in producing a taxonomic arrangement that will provide the necessary background for further field studies, breeding, and cytological investigation where these are needed for a more thorough analysis of relationships. The present treatment attempts only the preliminary organization aimed to point the way to such studies and attempts to discuss the problems that have arisen during the preparation of the manuscript for the treatment of the genus *Gilia* in Abrams, Illustrated Flora of the Pacific Coast States. Those species that have presented no particular problems have been omitted from this discussion as are also the general key and the formal descriptions. All of these are included in the treatment in the above mentioned flora.

THE TAXONOMIC ENTITIES

It is our firm conviction that the main objective of taxonomy is to give expression to the interrelationships that the taxonomist construes to exist in the group of plants under investigation. It would indeed be wonderful if the taxonomic categories with which he had to deal were each discrete with values fixed by definition or by legislation and utilized characters that offered no great problems in their interpretation. The interrelationships that are apparent in *Gilia* are exceedingly complex and display much intergradation. In some of the subgenera, races of almost every conceivable taxonomic magnitude exist ranging from the small population with one or two distinctive characters to what we choose to regard as species, and groups of species within the subgenera. Whether we look upon this complex in terms of morphological characters, evident crossability or any of the many aspects of ecological differentiation, the same complex situation exists. It is not a gradient of variation but rather a mosaic of interlocking centers of variation wherein groups of greater or less distinctness are evident and are distinctive because of any of several variants which may involve either morphology, behavior pattern, or ecology. To sort out these entities and express them in terms of values construed to designate or to delimit such categories as species or subspecies would serve only to fit into these categories groups of populations that are obviously of a very heterogeneous nature. Species and subspecies can only be applied to such groups in the relative sense in which they are outlined in the International Rules of Botanical Nomenclature (1935, Arts. 10, 12). What we may designate as species another may regard as subspecies and what we may designate as subspecies another will construe to be species. Taxonomic evaluation is only a tool for the expression of relationship and it is not too important that two workers agree precisely upon it if by their diverse concepts they arrive at the same pattern of relationship. We hope that in the entities that we have designated as species we have included groups of populations that possess a reasonably high degree of morphological uniformity correlated with a range of physiological capacity that expresses itself in a particular pattern of ecological and geographical distribution. Judging from the presence of intermediates between these groups of populations, they produce hybrids which become established in nature. On the other hand, these same groups either do not hybridize with other populations, or if they do, the progeny fail to establish themselves in the dispersal range of the seed producing parent. Where species would be so large as to become unwieldy for practical taxonomic use we have not followed a strict interpretation of this philosophy. Our chief objective has been to orient the entities so as to depict and characterize constellations of relationship as we see them.

Since little is to be gained by postulating relationships below the rank of subspecies without the aid of genetic manipulation of representative material, the present treatment is not carried below the level of subspecies. We do not imply by this that we regard the category "subspecies" and "variety" as being synonymous but rather that we accept both in the sequence as outlined in the International Rules of Botanical Nomenclature (1935, Art. 12). Every individual plant is potentially a member of every category in the taxonomic structure and although we list varieties under our subspecies and make new combinations involving subspecies we do not imply by this that the variety is raised to the level of subspecies or submerged in synonomy with the subspecies or the species. Technically the variety is at least part of the subspecies or the species. We include it in our literature citations only for bibliographic completeness.

Gilia ranges from southern British Columbia southward through the mountains and valleys into Mexico, thence eastward across Texas to the south Atlantic Coast. It is adventive as far north as Massachusetts. It recurs along the west coast of South America from Peru to Patagonia. The great preponderance of species, however, occurs in the arid regions from southern California to western Texas and northward into the Great Basin, with the Colorado and the Mohave deserts being especially rich in species. Although *Gilia* is predominantly a North American genus, it was first described by Ruiz and Pavon and was based upon the Peruvian species *G. laciniata.* It is named in honor of Felipe Luis Gil, a Spanish botanist. The following description outlines our concept of the constitution of the genus.

Gilia Ruiz and Pavon, Prodr. Fl. Peru, 25: t. 4. 1794.

Annual, biennial, or perennial herbs, rarely subshrubby. Leaves alternate, herbaceous rarely slightly rigid, entire or variously pinnately lobed, toothed, or dissected, often disposed in a basal rosette. Flowers solitary on slender pedicels in the leaf axils, or in paniculately branched or thyrsoid inflorescences, or congested in glomerules or sessile in capitate heads. Calyx lobes

usually equal, cleft nearly to the base and often flanked on the margins by a membrane, that of adjoining sepals often uniting to form a pseudotube which becomes distended or ruptured by the growing capsule. Corolla funnelform or salverform or less often campanulate, usually regular, rarely slightly irregular, blue, pink, red, yellow or white. Stamens equally inserted on the corolla tube or the throat, most often in or just below the sinuses of the corolla lobes, sometimes unequally inserted, usually equal in length, rarely unequal. Capsule 3-celled, the valves remaining joined at the base and campanulately spreading on dehiscence. Seeds usually several to many in a locule, rarely 1 or 2, rapidly taking up water when wetted and becoming mucilaginous on the surface, rarely not so affected.

For the most part relationships within the genus aggregate the species into fairly distinctive groups which have been variously treated as sections or as subgenera at the hands of several botanists. Most of these subgenera as here utilized are natural, although to treat them so it has been necessary to confine the application of some of them to a few or even single species. To do otherwise would frustrate our announced objectives. In a few of the subgenera we were strongly tempted to break them entirely from *Gilia* as separate genera but it soon developed that it would be more difficult to give expression to the interrelationships between such groups if they were so separated. The following key will serve to differentiate the subgenera.

Key to the Subgenera

Seeds very many to a locule, ellipsoidal, reddish brown, not mucilaginous when wetted; leaf blades chiefly broadly elliptic sometimes shallowly lobed, dentate, the teeth often aristate, plants annual or perennial .... Subgenus *Gilmania*

Seeds several to a locule, rarely one or two, usually mucilaginous when wetted; leaves variously dissected or lobed or entire, rarely with a broad elliptic blade.

Plants biennial or perennial, if annual, the inflorescence leafy-bracted.

Corolla 20–30 mm. long, red, pink, yellow, or white; inflorescence a thyrsoid panicle ... Subgenus *Ipomopsis*

Corolla 4–10 mm. long, white; inflorescence capitate-congested or glomerate, usually leafy-bracted .... Subgenus *Elaphocera*

Plants annual.

Ovules 1 or sometimes 2 to a locule; leaves irregularly toothed or lobed or lanceolate-entire; stamens unequally inserted on the long, narrow throat .... Subgenus *Greenianthus*

Ovules several to a locule, stamens usually equally inserted on the throat or tube or in the sinuses of the corolla lobes; leaves various.

Leaves variously toothed, lobed, dissected, or divided, rarely entire; flowers in paniculate, thyrsoid, glomerate or capitate inflorescences, rarely solitary in the upper leaf axils.

Stems conspicuously leafy, leaves becoming reduced only high in inflorescence; throat usually full campanulate, often equal or longer than tube; basal rosette rarely well differentiated at maturity of plant; inflorescence often capitate .... Subgenus *Capitata*

Stems not conspicuously leafy, cauline leaves much smaller than basal, basal rosette prominent; throat usually ample and short, less commonly as long or longer than the elongate tube; inflorescence never capitate ....

Plants with one to several erect stems usually branching above; corollas usually with elongate tubes; basal leaves strap-shaped or dissected, usually 2–10 cm. long .... Subgenus *Eugilia*

Plants low and divaricately spreading; corollas with short tubes, sometimes the throat elongate; basal leaves ovate to ovate-lanceolate, rarely over 1 cm. long .... Subgenus *Campanulastrum*

Leaves, or most of them, linear to linear-filiform, rarely a few pinnately dissected into few filiform lobes, never broad and toothed; flowers solitary in the leaf axils.

Corolla tubular to narrow funnelform, pink, white or pale blue .... Subgenus *Kelloggia*

Corolla open campanulate .... Subgenus *Tintinabulum*

Subgenus **Gilmania** subgen. nov.

Annua aut perennis, laminis foliorum latis, simplicis, dentatis vel lyrati-lobatis aut partitis, dentes subulatis vel aristatis; corollis parvis splendidis-rosaceis; multispermatis subrubris-fulvis.

Annual or perennial, leaf blades broad, simple, toothed, or lyrately lobed or parted; the teeth subulate to aristate; corollas small, bright pink; seeds many, reddish brown. Type. *Gilia latifolia.*

The subgenus *Gilmania* is composed of two well-marked species differing in several details though obviously closely related to one another. *Gilia latifolia* Gray is an annual and *G. Ripleyi* Barneby (*G. Gilmani* Jepson) is a perennial. They have in common the very many ellipsoid seeds to a capsule, each of which is pigmented with a red-brown color, the broad leaf blades with their aristiform teeth, and the numerous, small, pink corollas. It is one of the most distinctive groups within the genus yet its inclusion in *Gilia* seems beyond question, since it ties in closely with *G. leptomeria* of the subgenus *Eugilia.*

Subgenus IPOMOPSIS (Michaux) Milliken, Univ. Calif. Publ. Bot. 2: 24. 1904

The species included in this group were regarded by Michaux as constituting a distinct genus based upon the eastern *Gilia rubra.* Bentham included it under *Gilia* as a subgenus, a position that clearly expresses the relationships of its species. The biennial character of the members of this subgenus is outstanding. The chief problem in the group centers in the *G. aggregata* complex wherein specific and subspecific segregation in the southwest is very complicated. In the Pacific Coast states, however, only typical *G. aggregata* occurs.

Subgenus ELAPHOCERA (Nuttall) Milliken, Univ. Calif. Publ. Bot. 2: 24. 1904

The members of this subgenus have been treated in detail under the heading "the *Gilia congesta* complex" by Constance and Rollins and will not be further elaborated here except to point out that the concept of the group is here expanded to include the annual species *G. polycladon.* The outstanding characters of the group include a short tubular or salverform white to pale blue corolla with short stamens in or just below the sinuses of the corolla lobes, capitate or leafy-bracted, glomerate inflorescences and 1- to 2-seeded capsule locules. The species may be annual or perennial, herbaceous or shrubby.

Subgenus **Greenianthus** subgen. nov.

Annua, foliis integeris vel irregulariter aut regulariter pinnatisectis aut furcatis; corollis tubiformibus infundibuliformibus, jugulus angustissimatis tubis multo longiore; staminis inaequalisinsertatis, longitudine inaequalis; loculis 1- raro 2-ovulatis.

Annuals, leaves entire to irregularly or regularly pinnately cleft or forked. Corolla tubular, funnelform, throat very narrow, much longer than tube. Stamens unequally inserted on throat, unequal in length, locules 1-seeded rarely 2-seeded. Type. *Gilia gilioides.*

This subgenus is characterized by its broad, cleft or entire leaves with lanceolate teeth or lobes of very diverse size but never dissected into linear filiform segments. The usually deep violet to purple or sometimes white corolla is likewise distinctive with its very long, almost tubular throat and very unequally inserted stamens. The subgenus includes the *Gila gilioides* complex and the desert species *G. depressa.* This latter species presents no problem so will not be further dealt with here.

Although there is great morphological, genetical, and ecological diversity within *Gilia gilioides,* it stands as one of the most distinctive units within the genus *Gilia.* Its unequal and unequally inserted stamens together with the usual condition of uniovulate locules serve to set it apart from the rest of the genus. In fact, on the basis of these characters, it was once placed in *Microsteris,* and because of its general leafiness which extends well up into the inflorescence, in addition to the stamen and ovule characters, Bentham at one time included it in *Collomia.* On the other hand, its calyx and corolla and the nature of the capsular dehiscence as well as the lobing and alternate insertion of the leaves clearly indicate its close relationship with the other species of *Gilia.* Erection of a separate genus for *G. gilioides* would only serve to defeat the objectives of taxonomy by separating it from its obvious relatives. Despite the wide geographic range of the species and the variation that exists within it, a synonomy of only fourteen names is recorded in our treatment.

GILIA GILIOIDES subsp. **volcanica** (Brand) comb. nov. *G. divaricata* var. *volcanica* Brand in Engler, Pflanzenreich 4^{250}: 94. 1907.

This subspecies, with its pink corolla lobes, purple throat, and portion of the stamens exserted from the corolla tube is here regarded as having sufficient supplementary characters to warrant nomenclatural status. The geographic ranges of this and other color races usually do not overlap. Exceptions are a violet race and a white race in the middle altitudes of the Sierra Nevada which usually occur alone but sometimes are found intermixed. When occurring together, they seem to retain their distinctness.

Leaf variation, although extreme, does not manifest itself along lines that could be expressed in terms of taxonomic divergence. Variation occurs in both form and size of leaves. They may be simple, lanceolate, and entire or they may be irregularly cleft into 2 to several divisions or they may be toothed. Some may be regularly pinnately cleft. A population rarely may exhibit relative uniformity as to leaf character but it is not uncommon for a single large plant to display the entire range of leaf type variation found in the species as a whole.

Another point of variation pertains to stamen insertion and exsertion. Throughout most of the populations the stamens are usually all included although they may be unequally inserted and equal or slightly unequal in length. In *G. gilioides* subsp. *volcanica* one or two of the stamens are exserted and the remainder included.

GILIA GILIOIDES subsp. **glutinosa** (Bentham) comb. nov. *Collomia glutinosa* Bentham, Bot. Reg. 19: *sub* t. 1622. 1833.

Throughout southern and insular California as well as in northern Baja California a population with all of the stamens exserted has been variously treated in the literature. It has been described as *Collomia glutinosa* Benth. and as *Gilia Traskeae* Eastwood. Its morphological distinctness and geographic unity warrant its inclusion in a subspecific status.

Geographically *Gilia gilioides* ranges from northern Baja California to southern Oregon and eastward into Nevada. It occurs from sea level to near timberline throughout a great range of habitats.

The remainder of the synonymy of the group is regarded as reflecting chiefly the changes in nomenclatural status of members of the group hence will not be further discussed here.

Subgenus Capitata Milliken, Univ. Calif. Publ. Bot. 2: 37. 1904.

This is a very natural subgenus characterized by leafy stems with the leaves little reduced upward and with highly dissected blades and by flowers with usually full campanulate throats and short tubes. The calyces are often woolly. The group can be divided into two main types on the basis of the fact that in some plants the inflorescence is a compact head while in others it is made up of open glomerules or of solitary peduncled flowers. Under certain habitat conditions however, some species normally producing heads develop instead open paniculate inflorescences. The members of this subgenus lend themselves to manipulation genetically since they are adaptable to garden culture and since the seeds display a high percentage of germination. Cytogenetic work on this problem is at present being carried on by students; so we shall confine our remarks only to those points that demand our immediate attention and await a fuller report on the problem. It will suffice here to point out that five different specific names have been applied within the group of plants that we include under *Gilia achilleaefolia*. These are *G. achilleaefolia* Benth., *G. stricta* Scheele, *G. abrotanifolia* Nuttall ex Greene, *G. staminea* Greene, and *G. chamissonis* Greene. Of these, *G. stricta* is of horticultural origin, probably derived directly from seed of *G. achilleaefolia* sent to Europe by Douglas. The remainder vary geographically to such an extent that it is impossible to clearly differentiate them. We therefore for the present accept the following:

Gilia achilleaefolia subsp. chamissonis (Greene) Brand.

Gilia achilleaefolia subsp. **staminea** (Greene) comb. nov. *G. staminea* Greene, Erythea 3: 105. 1895.

Gilia capitata Douglas.

Gilia multicaulis Bentham, Bot. Reg. 19: *sub* t. 1622. 1833. The taxonomy of this species presents many complications resulting largely from its great diversity. Several variants have been described within the complex which we believe are best treated as subspecies since we are unable to clearly differentiate between them. *Gilia multicaulis* subsp. *eu-multicaulis* Brand is the common species of the central coast ranges. It produces flowers on short peduncles in few flowered glomerules, is exceedingly variable as to pubescence and its ascending or erect stems are quite leafy well up into the inflorescence.

GILIA MULTICAULIS subsp. **peduncularis** (Eastwood) comb. nov. *G. peduncularis* Eastwood ex Milliken, Univ. Calif. Publ. Bot. 2: 34. 1904.

Often growing with typical *G. multicaulis* but occurring independently also is the form with the flowers on elongate slender peduncles. It intergrades with the typical form in this character, but differs in being much less leafy.

GILIA MULTICAULIS subsp. **millifoliata** (Fischer & Meyer) comb. nov. *G. millifoliata* Fischer and Meyer, Ind. Sem. Hort. Petrop. 5: 35. 1838.

This is a stout, glandular, divaricately branched type with an accrescent calyx which occurs along the coastal sand dunes from central California to southern Oregon.

GILIA MULTICAULIS subsp. **Nevinii** (Gray) comb. nov. *G. Nevinii* Gray, Syn. Fl. N. Am. ed. 2, 2 (suppl.): 411. 1886.

On San Clemente and Guadalupe Islands occur populations striking because of their finely dissected leaves and corollas much longer than in the type. They were first described by Gray as *Gilia multicaulis* var. *millifolia,* and later raised to specific rank by Gray under the name *G. Nevinii.* Since the name "*millifolia*" is so close in orthography and pronounciation to the preceding subspecies and since we apply it to another rank we believe it expedient to accept Gray's name in the role of a trinomial.

GILIA TRICOLOR Bentham.

GILIA TRICOLOR subsp. **diffusa** (Congdon) comb. nov. *G. diffusa* Congdon, Erythea 7: 186. 1900. *G. tricolor* var. *longipedicellata* Greenm., Rhodora 6: 154. 1904. *G. inconspicua* subsp. *sinuata* var. *oreophila* subvar. *diffusa* Brand, Pflanzenreich 4^{250}: 105. 1907.

Occurring occasionally in the range of the species but extending farther south in the Sierra Nevada foothills and in the hills bordering the southern San Joaquin Valley, this subspecies is recognized for its diffuse branching and its smaller flowers which are borne on longer, slender pedicels.

Subgenus EUGILIA (Bentham) Milliken, Univ. Calif. Publ. Bot. 2: 23. 1904

The subgenus *Eugilia* is the major problem in the genus *Gilia.* It occurs chiefly in the deserts and semi-arid basins and valleys of the west and southwest with some races extending well up into the intervening mountains, and reaches the Pacific Coast in sand dune areas from Santa Cruz County, California, southward.

To one beginning a study of this group certain features stand out. Most obvious is the strong tendency for parallel variation among the entities of this complex. Many of the entities comprise small-flowered subspecies with short corolla tubes and large-flowered subspecies with long corolla tubes. Examples of such parallel variation are: *G. splendens* and its long-corolla-tubed form, *G. splendens* subsp. *Grinnellii; G. latiflora* and its long-corolla-tubed form *G. latiflora* subsp. *speciosa.* Nevertheless intergradation between these species and subspecies occurs.

The subgenus breaks clearly into two well-marked subdivisions between which we have seen no evidence of intergradation. The most obvious differentiating character has been overlooked in the past largely because it involves a character that in many groups is often unstable, namely the character of the pubescence. *Gilia Abramsi, G. ochroleuca, G. tenuiflora, G. latiflora* and *G. sinuata* have in common a pubescence consisting of long, tangled hairs so fine that an individual hair is not readily seen with the naked eye. This pubescence is found mainly on the lowermost leaves and stems and may be thick and woolly or tufted or very sparse. In a few cases where relationships to one or another of these five species are clear through other characters, the plants may be entirely glabrous. In contrast to this situation the other members of the subgenus, *G. splendens, G. caruifolia, G. stellata, G. scopulorum* and *G. leptomeria,* have a pubescence of coarse hairs of various types but never long and tangled. The individual hairs may be readily seen with the naked eye. A completely glabrous condition is unknown to us in this section of the subgenus.

One of the most baffling problems in taxonomic treatments of the subgenus *Eugilia* has been the variation in the nature of the leaves. The numerous distinct leaf forms which occur in various combinations with the characters of leaf size and degree of pubescence suggests that there are numerous races within a species. Considerable variation, moreover, can be seen in a single population. It has been our observation that in any given population the larger the individual the more complex the dissection of the leaf; and in two populations, related, but of distinctly different leaf form, the smallest individuals may appear quite similar. The situation in *Gilia latiflora* will provide an example. Specimens in one mass collection displayed leaf types 1, 4 and 5 (text fig. 1) in the order of their development from simple to complex whereas another such collection displayed types 1, 2 and 3 (text fig. 1). In the first case the most highly developed leaves were bi- to tri-pinnate with narrow rachis and in the second case the most highly developed ones were bipinnate with broad rachis. In both cases plants bearing only leaf type 1 were indistinguishable. This suggests that the degree of dissection of the leaves may be related to the rate of growth as influenced by local ecologic differences or seasonal differences. In a poor flowering year on the desert such potential leaf variation is masked and to make certain of the type of plant being dealt with in any season, one must look for the better-developed individuals.

In *G. latiflora* an attempt was made to correlate leaf form with other characters and with geographic distribution, and this was

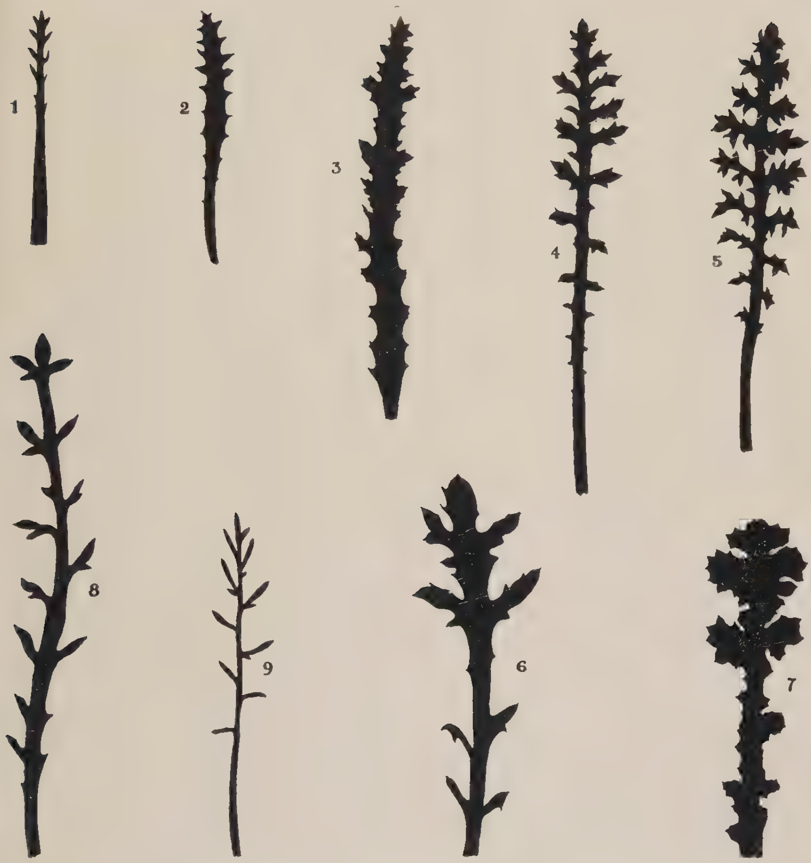

FIG. 1. Leaf types in *Gilia,* subgenus *Eugilia.* 1, *G. latiflora,* 1 mile east of Lancaster, Los Angeles County, California (*Mason 6869*); 2, *G. latiflora,* Barstow, San Bernardino County, California (*W. W. Jones,* April 15, 1921); 3, *G. latiflora,* 5 miles west of Barstow, San Bernardino County, California (*Minthorn 80*); 4, *G. latiflora,* Kramer Station, San Bernardino County, California (*Constance & Mason 2110*); 5, *G. latiflora* subsp. *speciosa,* summit between Nine Mile Canyon and Kennedy Meadows, Tulare County, California (*Alexander & Kellogg 2962*); 6, *G. latiflora,* 2.5 miles east of Coso Hot Springs, Coso Range, Inyo County, California (*Alexander & Kellogg 2771*); 7, *G. latiflora* subsp. *cana,* Carroll Creek, southwest of Lone Pine, Inyo County, California (*Alexander & Kellogg 2814*); 8, *G. tenuiflora* subsp. *interior,* Red Rock Canyon, Kern County, California (*Mason 9278*); 9, *G. ochroleuca,* Carrizo Plain, San Luis Obispo County, California (*Esau,* April 13, 1935). All drawings × 1.

possible in the subspecies; but the situation of typical *G. latiflora* in the Mohave Desert presents a confused picture. In the area between Victorville, Barstow, and Lancaster, California, collections display specimens similar in most of their features except leaf form; yet here every one of the first six types depicted in text fig. 1 is represented, and these vary widely in dimension as well as dissection so that in their vegetative characters the plants appear very different. To one who is familiar with the *G. latiflora* complex in the herbarium and who has had only a limited experience with it in the field the impression is carried that there are more species in the herbarium than there are in the field. The literature reflects this situation. Although we have corrected some of the fallacies inherited from previous treatments, only detailed population studies will furnish us with a true picture of variability in the *G. latiflora* complex.

In the past the small flowered types in the subgenus *Eugilia* have generally been regarded as centering around what has been termed *Gilia inconspicua,* an epithet which we reject because of the difficulty of establishing just what is the type upon which the name rests. The case for this decision has been presented by the senior author (1945) and will not be further elaborated here. We construe most of these small flowered plants to group themselves around three well-marked species, namely *G. ochroleuca* Jones, *G. sinuata* Douglas, and *G. leptomeria* Gray, centering geographically in the Great Basin and desert areas south to northern Baja California. The remainder of the group in the past has been variously treated as many distinct species or has been aggregated under *G. tenuiflora* or *G. latiflora* as synonyms or as varieties.

The outstanding characters of the subgenus *Eugilia* are the annual habit, the usual varied leaf dissection, the basal rosette (except in depauperate individuals), the much-reduced cauline leaves, the stems appearing almost naked, the subglomerate to open-paniculate, stipitate-glandular inflorescences, and the stamen insertion in the sinuses of the corolla lobes (one exception). Following is a discussion of the individual species.

Gilia splendens Douglas ex Paxton, Mag. Bot. 3: 260. 1837.

This is the species that has been regarded in the literature as *G. tenuiflora* var. *altissima* Parish. The name *G. splendens* as applying to this seems to have been overlooked in spite of the excellent illustration in Lindley's Botanical Register (1836, t. 1888) under the caption "*G. tenuiflora* Benth." This illustration was made from living plants grown in England from seed collected by David Douglas and labelled by him "*Gilia splendens*" and is a faithful reproduction of the species. The range of *G. splendens* barely overlaps into the range of *G. tenuiflora* but we have seen no evidence of intergradation between them. *Gilia splendens* is readily distinguished from that species by its pubescence of coarse translucent hairs on the basal leaves, the bi- and tri-pinnate basal leaves with finely toothed lobes and the rose or bright pink color of the corolla as opposed to the purple and yellow of *G. tenuiflora.* It is typically a montane species occurring from the mountains of southern Monterey County to those of Santa Barbara and Ventura counties and in the San Gabriel, San Bernardino, and San Jacinto mountains, California.

Gilia splendens subsp. **Grinnellii** (Brand) comb. nov. *Gilia Grinnellii* Brand in Engler, Pflanzenreich 4^{250}: 101. 1907.

This is a long-tubed form of the species that seems to be restricted to the San Gabriel and San Bernardino mountains, California.

Gilia splendens subsp. **australis** subsp. nov. A *G. splendens* differt capsulis magnioris (5–7 mm. longis) et corollis multis brevioris quo limbis est longioris proportionalis tubis et jugulis.

Differs from *G. splendens* in the larger capsules (5–7 mm. long) and in the much shorter corolla in which the limb is proportionately longer.

San Bernardino and Riverside counties, California, to Baja California, Mexico.

Type. Temecula Valley, Riverside County, California, *Mason 3195* (Herb. Univ. Calif. 748763).

Gilia caruifolia Abrams, Bull. Torrey Bot. Club 32: 540. 1905.

Gilia caruifolia resembles *G. splendens* closely in vegetative aspect, but differs in the smaller blue, violet, pink or white corolla with a short throat and long stamens inserted midway on the throat. All other species of the subgenus *Eugilia* have the stamens inserted in the sinuses of the corolla lobes. Their geographic distributions are completely distinct, *G. caruifolia* occurring farther to the south. The gap between their ranges is filled by *G. splendens* subsp. *australis* which occurs also farther south in the region of *G. caruifolia.* Throughout its range this subspecies maintains the corolla tube and throat proportions and stamen character of *G. splendens* but the smaller flowers give a suggestion of its intermediate nature between *G. splendens* and *G. caruifolia.*

Gilia stellata Heller, Muhlenbergia 2: 117. 1906. *G. tenuiflora* var. *Newloniana* Jepson, Fl. Calif. 3: 179. 1943.

The form of the lower leaves as well as the flower size and color clearly mark this species as related to the interior form of *G. splendens.* It differs in its peculiar pubescence of several-celled, translucent, geniculate hairs and much smaller corollas. It is primarily a desert species rather than a montane plant.

Gilia scopulorum Jones, Bull. Torrey Bot. Club 8: 70. 1881. *Gilia scopulorum* and *G. stellata* are unusual in the subgenus *Eugilia* in that the calyx tends to be accrescent rather than to be ruptured by the capsule. Also they are unique in that even the highest cauline leaves tend to be toothed rather than reduced to an entire bract. They also have spherical rather than the cylindric capsules, like *Gilia splendens* and *G. caruifolia.* They may be readily distinguished from one another by the broader leaf segments and long corolla tube of *G. scopulorum* and by the geniculate hairs of *G. stellata*. *Gilia scopulorum* occurs chiefly in washes in the canyons of desert mountains.

Gilia leptomeria Gray, Proc. Am. Acad. 8: 278. 1870.

This species is outstanding among the small flowered members of the subgenus *Eugilia* because of its broad leaf blades and its pubescence. The leaf blades when lobed or dissected have the lobes opposite or sub-opposite, a condition not typical of the other members of the subgenus. The cauline leaves are simple and entire. In pubescence, *G. leptomeria* possesses glandular hairs, not only in the inflorescence as in the other species but on the basal leaves as well. There have been frequent references to trident-lobed flowers in this group of *Gilia*. All such specimens known to the writers are referable to *G. leptomeria*. They are *G. leptomeria* var. *tridentata* Jones, *G. inconspicua dentiflora* Davidson, *G. leptomeria* var. *myriacantha* Jones, *G. triodon* Eastwood, and *Aliciella triodon* (Eastwood) Brand. This latter impressed Brand sufficiently to cause him to segregate it as a distinct genus. It has been the experience of the senior author in the field that this form of the petals occurs on soils high in gypsum. The difference though no doubt genetic scarcely warrants subspecific status.

In addition to typical *Gilia leptomeria* the following subspecies seem to warrant recognition:

Gilia leptomeria subsp. **micromeria** (Gray) comb. nov. *G. micromeria* Gray, Proc. Am. Acad. Sci. 8: 271. 1870.

The pedicels are more slender than in the species and are often reflexed, the corolla is often minute and the petals sometimes are 3-toothed but usually entire. The opposite leaf lobes and the entire, upper cauline leaves clearly place this with *G. leptomeria*. It ranges from eastern Oregon to the Rocky Mountains, the type having come from the hills above Bear River near Evanston, Utah.

Gilia leptomeria subsp. **rubella** (Brand) comb. nov. *G. arenaria* var. *rubella* Brand in Engler, Pflanzenreich 4^{250}: 103. 1907.

The basal leaves of this subspecies are more deeply cut than in the species and are often bipinnate. The literature displays some confusion as to the red pigment in the stems which resulted in the name applied by Brand. Rydberg, under *G. Hutchinsifolia* (Bull. Torrey Bot. Club 40: 472. 1913) maintains Brand confused red sand with plant pigment. We noted a red coloration on the base of the stems in all collections seen, including the specimen upon which *G. leptomeria* subsp. *rubella* rests (*Jones 1651*). Here again the entire cauline leaves and the opposite lobes of the basal leaves clearly relate this to *G. leptomeria*. It is known from Red Rock Canyon in Kern County, California, east to southern Nevada, Utah and northern Arizona.

Gilia ochroleuca Jones, Contrib. West. Bot. 8: 35. 1898.

There are three outstanding features whereby this species may be readily distinguished from other small flowered species namely, (1) the linear segments or dissections of the basal leaves, (2) the linear, finger-like lobed cauline leaves, and (3) the yellow or cream colored flowers whose lobes sometimes are tipped with violet. Although we designate only two subspecies for the Pacific Coast States we are aware of some interesting developments in this species in southwestern Nevada and Arizona which deserve further study.

GILIA OCHROLEUCA subsp. **typica** stat. nov.

Leaf rachis and lobes almost filiform, not exceeding 1 mm. in width; inflorescence full, divaricately much branched, branches filiform. This subspecies is based upon the type of the species and is the least widespread of the two subspecies, being restricted to the Mohave and Colorado deserts and the hills of Inyo County, California, and the southwest border of Nevada.

GILIA OCHROLEUCA subsp. **transmontana** subsp. nov. Lobis foliorum 1–2 mm. latis, primibus ramis inflorescentium virgatis, inflorescentibus angustatis.

Leaf lobes 1–2 mm. wide, main branches of the inflorescence virgate, the inflorescence narrow.

Eastern Washington and Oregon southeast of the Sierra Nevada to the mountains of southern California and northern Baja California, Mexico; east to Wyoming, Utah and New Mexico.

Type. Beaver Dam River, Arizona Strip, Arizona, *Maguire et al. 4923* (Herb. Univ. Calif. 553752).

GILIA SINUATA Douglas ex Bentham, in DC. Prodr. 9: 313. 1845.

Gilia sinuata is an exceedingly variable species particularly in leaf dissection and degree of pubescence. It differs from *G. ochroleuca* chiefly in the bract-like cauline leaves, the short-toothed lobes of the basal leaves, and the proportionately longer corolla tube. Its stems are usually stout.

Although *G. ochroleuca* and *G. leptomeria* differ widely from each other in leaf form and pubescence and offer no difficulties in identification, there are two lines of evidence making the possibility worth considering that chance interbreeding of these two species has given rise to at least the ancestors of *G. sinuata.* (1) A study of the geographical distributions of these hypothetical parents shows that they occur sympatrically in the central and eastern Great Basin area, but *G. ochroleuca* extends a little farther west than does *G. leptomeria.* On the western margins of the range of *G. leptomeria* can be found also *G. sinuata* but to our knowledge it does not occur east of here. In eastern Washington and Oregon, where there are no other species of the section to confuse the issue, it may be significant that *G. sinuata, G. ochroleuca,* and *G. leptomeria,* have been collected from the same localities and in some cases, at least, *G. ochroleuca* and *G. sinuata* have been mixed in the same collections. (2) In respect to its leaf characters, *G. sinuata* is intermediate between *G. leptomeria* and *G. ochroleuca.* The characters in question can be most easily compared if presented in tabular form.

Table 1. Comparison of Leaf Characters

Characters	*G. leptomeria*	*G. sinuata*	*G. ochroleuca*
Basal leaves	broadly strap-shaped, sinuately toothed or shallow lobed.	pinnate or bipinnate with rachis broad and shallowly to deeply cut into lobes which are not linear.	pinnate or bipinnate with narrow rachis and slender, linear lobes, which are longer than 2 times the width of the rachis.
Cauline leaves	entire or shallow-toothed; abruptly smaller than basal leaves, the stems appearing almost naked above the prominent basal rosette.	similar to basal leaves but gradually or abruptly shorter; the stems somewhat leafy, or appearing almost naked.	simple pinnate with narrow rachis, the lobes linear and longer than 2 times width of rachis; the leaves shorter than basal ones, but not abruptly so, stems appearing somewhat leafy.

In southwestern Nevada and southern California *G. sinuata* has reached a more complex state of development than in the north, due in part, at least, to the comparative abundance of related species as a source of new characters, and to the more varied geography and ecology of the region, providing a wide choice of habitats for new forms. In this region of overlap, *G. sinuata* grows side by side with its close relative, *G. latiflora,* and the two forms seem to hybridize freely.

Gilia Abramsii (Brand) comb. nov. *G. arenaria* var. *Abramsii* Brand in Briquet, Ann. Conserv. et Jard. Bot. 15–16: 330. 1913.

Gilia Abramsii appears to differ from *G. ochroleuca* principally in the nature of the corollas which are larger with abruptly expanding, conspicuous throat. Although it is known to have occasional intermediates with *G. ochroleuca,* its distribution is distinct, being at higher elevations to the west and south of *G. ochroleuca.*

Gilia Abramsii subsp. **integrifolia** subsp. nov. Foliis inferioribus plerumque simplicis et integeris, linearis, per occasionem aliquot cum 1–2-lineari-lobis.

Basal leaves mostly simple and entire, linear, occasionally a few with one or two linear lobes.

Type. Temecula Canyon one mile south of Temecula, Riverside County, California, *Mason 3112* (Herb. Univ. Calif. 748762).

GILIA TENUIFLORA Bentham, Bot. Reg. 19: *sub* t. 1622. 1833.

We include in synonymy with *G. tenuiflora* what has been described as *G. arenaria* of Douglas collected presumably at Monterey, California. We have seen specimens from the Del Monte sand dunes and from sandy hills in the Santa Cruz Mountains. They differ only in having the lobes of basal leaves reduced. Recent mass collections have shown both leaf types to occur in the same populations, the reduced-lobe type occurring particularly in depauperate specimens. The type of *Gilia arenaria* is evidently just such a specimen; thus we consider the two names synonymous.

GILIA TENUIFLORA subsp. **interior** subsp. nov. Caulis erectis, e basi ramosissimis divaricatis, foliis inferiore vix longiore; foliis levi-vel moderate-lanatis; corolla 6–14 mm. longis, calycis 2–4-plo longiore, tubis 3–5 mm. longis purpureo, jugulo flaveo 5-purpure-maculoso infra lobus palide-violescens.

Stem erect, much branched and spreading from the base, barely exceeding the basal rosette; leaves lightly to moderately woolly pubescent; corolla 6–14 mm. long, 2–4 times the calyx, tube 3–5 mm. long, purple, throat yellow with 5 purple spots subtending the light violet lobes.

Inner coast ranges from Mount Hamilton to Santa Barbara County, southern San Joaquin Valley to the mountains of Kern County and the western Mohave Desert, California.

Type. Walker Pass, Kern County, California, *Mason 8340* (Herb. Univ. Calif. 748761).

Gilia tenuiflora as here interpreted is a variable entity both in corolla size and proportions and in leaf characters. In an inland direction corollas tend to become smaller, and towards the south the outstanding tendency is toward a proportionate shortening of the corolla-tube. Thus, in Monterey County, California, in the northern part of its range, where the type of the species originated, the corolla tube may attain a length of three times greater than the throat; but in the southern part of its range, in the Cholame Valley, Kern County, and in the northwestern reaches of Antelope Valley, Los Angeles County, where *G. tenuiflora* intergrades with *G. latiflora,* the corolla proportions gradually approach those of *G. latiflora,* namely the tube is less than two times the throat, and the throat is more broadly expanding.

The leaf form is typically similar to that of *G. ochroleuca,* being pinnately or bipinnately lobed with slender linear lobes and a linear rachis, but frequently the lobes of the basal leaves are reduced to teeth as previously discussed. The most constant leaf feature is the fingerlike, linear lobes of the cauline leaves.

The inland transition of *G. tenuiflora* toward smaller corolla size and also more diminutive habit reaches its ultimate in *G. tenuiflora* subsp. *interior.* Were it not for the purple and yellow coloration of the corolla, as in typical *G. tenuiflora* one would confuse the subspecies with *G. ochroleuca;* since its flowers are small enough to be within the upper limits of the size range for *G. ochroleuca* flowers, and like the typical *G. tenuiflora,* it possesses the type of cauline leaf so characteristic of *G. ochroleuca.*

As one observes the aspect of this subspecies in its range from north to south he finds, as in typical *G. tenuiflora,* an intergradation with desert forms. In this case, however, not only *G. latiflora* but also *G. ochroleuca* influences the complex. It is significant that in mapping this group in the Mohave Desert we found *G. tenuiflora* subsp. *interior* to occur only in localities where *G. ochroleuca* and *G. latiflora* also occurred. Furthermore, several collections are obviously heterozygous, as evidenced by the wide range in corolla length and leaf form. Detailed population studies are much to be desired for the whole desert complex.

Gilia latiflora Gray, Syn. Fl. 2(1): 147. 1878.

We have discussed some of the outstanding problems of leaf variation as they pertain to *G. latiflora.* Certainly without more detailed genetic studies and without more detailed field work, and taking into consideration the erratic seasonal conditions of the area, one can only express the range of variability of leaves and flowers and treat this highly polymorphic group as a single entity having in common corollas with short tubes and ample, broadly-expanding throats. There are, however, some outstanding variations that seem to be correlated with one another and seem to have distinctive patterns of geographic distribution.

Gilia latiflora subsp. **speciosa** (Jepson) comb. nov. *G. tenuiflora* var. *speciosa* Jepson, Fl. Calif. 3: 181. 1943.

This subspecies varies from the typical form in having an elongated corolla tube which may be as much as 4 cm. long, but which varies from 2–8.5 times the length of the throat. Its leaves may be of types 1, 4, 5, or 7 (text fig. 1). It occurs in the northern Mohave Desert where it integrades with typical *G. latiflora.* It likewise intergrades with *G. latiflora* subsp. *Purpusii.*

Gilia latiflora subsp. **Purpusii** (Milliken) comb. nov. *G. tenuiflora* var. *Purpusii* Milliken, Univ. Calif. Publ. Bot. 2: 29. 1904.

In many respects this subspecies gives the impression of being a small form of *G. latiflora* subsp. *speciosa.* The corolla tube, however, is more slender and the lobes narrower. Leaf types 1 and 4 (text fig. 1) are characteristic of it although the lobes tend to be somewhat shorter and more crowded than in type 4. It occurs in the southern Sierra Nevada in Tulare County, California.

Gilia latiflora subsp. **cana** (Jones) comb. nov. *G. latiflora* var. *cana* Jones, Contr. West. Bot. 8: 35. 1898.

The corolla tube of this subspecies varies from 2–3 times the throat. Its leaves are covered with a dense layer of white wool. This white wool and the broader leaf lobes (type 7, text fig. 1) distinguish it from *G. latiflora* subsp. *Purpusii* from which it is separated geographically by the crest of the southern Sierra Nevada. It intergrades with *G. latiflora* subsp. *triceps* to the east and with typical *G. latiflora* to the south. It occurs on the east slope of the Sierra Nevada in Mono and Inyo counties, California.

GILIA LATIFLORA subsp. **triceps** (Brand) comb. nov. *G. tenuiflora* var. *triceps* Brand in Engler, Pflanzenreich 4^{250}: 102. 1907.

This subspecies is outstanding for its full, many-flowered inflorescences and filiform corolla tubes. The leaves may be of types 5, 6 or 7 (text fig. 1). It occurs in the valleys and mountains east of the southern Sierra Nevada to southern Nevada and south to the San Bernardino Mountains, California.

GILIA LATIFLORA subsp. **leptantha** (Parish) comb. nov. *G. leptantha* Parish, Zoe 5: 74. 1900.

This subspecies resembles *G. latiflora* subsp. *Purpusii* in many characters but differs from it chiefly in the shorter corolla tube and in its long-exserted stamens. The leaves are of types 4 and 5 (text fig. 1). It occurs in the Mount Pinos region of Ventura County and in the San Bernardino Mountains, California.

GILIA LATIFLORA subsp. **exilis** (Gray) comb. nov. *G. latiflora* var. *exilis* Gray Syn. Fl. ed. 2, 2(suppl.): 411. 1886.

The corolla proportions of this subspecies are similar to typical *G. latiflora,* the tube being shorter than the long full throat. The flowers, however, are smaller and the whole plant is diminutive with numerous slender branches from the base. It intergrades with the type and occurs in the San Gabriel and San Bernardino Mountains, California.

Subgenus **Campanulastrum** (Brand) comb. nov.

Gilia subgenus *Greeneophila* Brand, section *Campanulastrum* Brand in Engler, Pflanzenreich 4^{250}: 144. 1907.

This subgenus, based upon *G. campanulata,* but construed by Brand as a section involving several species belonging to the genus *Linanthus,* is here restricted to include *Gilia campanulata* Gray and *G. inyoensis* Johnston. It is closely related to the subgenus *Eugilia* from which it differs in the short broad corollas, the low spreading form of the plant, and the broad short leaves.

Subgenus **Kelloggia** subgen. nov.

Folis plerumque linearibus vel lineari-filiformibus raro aliquot pinnatisectis in paucis filiformibus lobis; floribus solitariis axillis, corollis tubiformibus vel angustati-infundibuliformibus vel turbinatibus hic calycis vix longiore, alio modo calycis multo longiore.

Leaves, or most of them, linear or linear-filiform, rarely a few pinnately dissected into few filiform lobes, flowers solitary in leaf axils, corolla tubular to narrow funnelform, or turbinate, then barely exceeding the calyx, otherwise much exceeding the calyx. Based upon *G. capillaris* Kellogg.

This subgenus includes *G. leptalea, G. capillaris, G. minutiflora* and

G. tenerrima. Except for a subspecies of *G. leptalea* the leaves are all linear-filiform and entire. Of these species only *G. leptalea* needs special consideration here.

Gilia leptalea subsp. **pinnatisecta** subsp. nov. Speciei simili autem foliis pinnati- vel laciniati-lobatis aut dissectis, planta totus saepe glandulosus-viscidus.

Similar to the species but the leaves pinnately to laciniately lobed or dissected, and the whole plant often glandular-viscid. North Coast Ranges, Lake County to Humboldt County, California; San Marcos, Brandegee (Santa Barbara County?).

Type. Open ground about Whispering Pines resort, Lake County, California, *Baker 2299a* (Herb. Univ. Calif. 353868).

Gilia leptalea subsp. **bicolor** subsp. nov. Speciei simili autem jugulus flavus tubo subaequantibus.

Similar to the species, but the throat subequal the tube and yellow. Canadian zone; central Sierra Nevada, California.

Type. Dardanelle, Tuolumne County, California, *Alexander & Kellogg 3736* (Herb. Univ. Calif. 702227).

Subgenus **Tintinabulum** (Rydberg) comb. nov.

Tintinabulum Rydberg, Fl. Rocky Mountains, pp. 698 and 1065. 1917.

In view of the close relationship between the single species of this subgenus with the entire linear-leaved members of the subgenus *Kelloggia* it seems scarcely necessary to recognize *Tintinabulum* of Rydberg as a genus. It would stand only on the open campanulate yellow corollas of *Gilia filiformis.* There are occasional colonies with cream colored flowers.

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POTAMOGETON LATIFOLIUS IN TEXAS

W. C. Muenscher

In June, 1945, my attention was attracted by an abundant growth of an unfamiliar *Potamogeton* in the outlets of springs about Fort Stockton, in western Texas. When Dr. William T. Winne and I began to collect some of these specimens for pressing, it became apparent that we had a robust species belonging to the subgenus Coleogeton. A series of specimens brought back to the herbarium at Cornell University was determined as *Potamogeton latifolius* (Robbins) Morong, only after considerable study.

Potamogeton pectinatus var. *latifolius* Robbins (in S. Watson, Botany Kings Expl. p. 338. 1871) was described from material collected in running brackish waters of Humboldt River below Humboldt Lake, Nevada (*W. W. Bailey 1142*).

Potamogeton latifolius (Robbins) Morong (Mem. Torrey Bot. Club 32: p. 52, 1893) is based on the description of Robbins as amplified by Morong from fruiting material collected by Mrs. R. M. Austin in Goose Lake in northeastern California in 1884.

The only records of *Potamogeton latifolius* that could be found are from northwestern Nevada, northeastern California and southern Oregon.

Through the kindness of its officials, I have had an opportunity to examine the following specimens of *Potamogeton latifolius* in the Gray Herbarium: NEVADA. Humboldt Lake, 1867, *Bailey 1142;* Hot Springs, Nevada desert, 1874, *Lemmon 1164.* CALIFORNIA. Mono County, 1898, *Congdon 9915;* Kings River, 1876, *Lemmon 1521.* OREGON. Goose Lake?, 1897, *Everman.*

The Fort Stockton material, in all its essential features, compares with the above specimens. Thus, the Texas station represents a considerable extension of the recorded range of *Potamogeton latifolius.*

Good material of this species appears to be rare in herbaria. The only illustration that could be located, Morong (1893), is hardly adequate to permit it to be recognized as *Potamogeton latifolius.* The following description and illustration were both based upon the Texas collection (in running water, Comanche Springs, Fort Stockton, Pecos County, Texas, June 30, 1945, *Muenscher* and *Winne 16516*). Specimens have been deposited in the herbarium of Cornell University.

POTAMOGETON LATIFOLIUS (Robbins) Morong. Rootstock slender, long-creeping, about 2 mm. in diameter, rooting freely at the nodes. Stems simple below, repeatedly branched above, 30–100 cm. long, the ultimate branches mostly less than 10 cm. long and bearing 1 or more spikes. Leaves linear, somewhat crisp and fleshy, the blades 2–7 mm. wide, mostly from 3 to 7 cm. long, those of the basal leaves somewhat longer and those on the ultimate and spike-bearing branches often less than 3 cm. long, green to bronze, rather opaque; leaf margin entire; apex obtuse, rounded or mucronate to acute on the upper leaves; blade with 3 nearly-equal main nerves and often with 1 or 2 smaller nerves near each margin, reticulated by prominent cross-nerves between the main parallel nerves. Stipules 8 to 12 mm. long, scarious, adnate to the leaf-base to form a sheath; ligule about 1 to 4 mm. long, hyaline along the margin, entire or becoming erose. Ped-

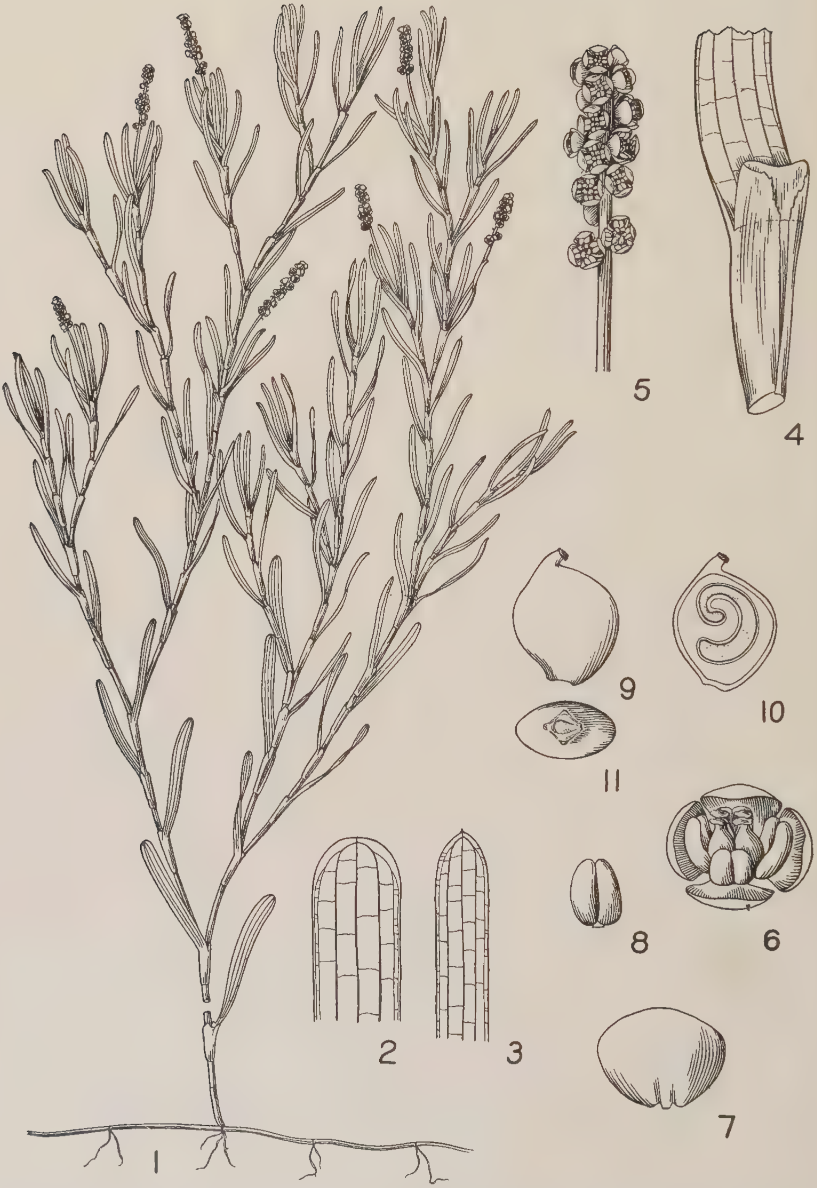

Plate 24. Potamogeton latifolius. Fig. 1, habit sketch; × 1/3. Fig. 2, apex of lower leaf; × 2. Fig. 3, apex of upper leaf; × 2. Fig. 4, leaf sheath; × 3. Fig. 5, spike; × 1. Fig. 6, flower; × 5. Fig. 7, sepaloid connective; × 8. Fig. 8, stamen; × 5. Fig. 9, fruit, surface view; × 3. Fig. 10, fruit, vertical section; × 3. Fig. 11, fruit, top view; × 3. Drawn from preserved material by Miss Elfrieda Abbe.

uncles 2–5 cm. long, 1–1.5 mm. in diameter, tapering above, green to bronze-red. Spike 2 to 3 (4) cm. long, dense, ultimately of 4 to 6 distant nodes with 2 or more flowers at each; basal internodes 5–12 mm. long, the upper shorter. Sepaloid connectives 1–1.5 mm. high, 2 mm. wide. Pollen grains spherical to elliptical in outline. Fruits olive-green to fulvous, 4 mm. long, 3 to 4 mm. broad, somewhat compressed but the sides convex; stigma somewhat capitate but oblique, on a short stout style in fruit; beak about 1 mm. long, slightly curved. No winter buds observed although some of the ultimate branches are abbreviated and fleshy and may function as such.

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THE PLACE OF WILLIS LINN JEPSON IN CALIFORNIA BOTANY

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For three-score years Willis Linn Jepson, 1867–1946, was actively connected with the Department of Botany of the University of California as student, professor, and professor emeritus. Throughout this long period he was thoroughly devoted to the study of the flora of his native state and to furthering its interpretation and appreciation. To this end he founded the California Botanical Society in 1913, which he served as president, with the exception of three years, until 1929. In 1916 he launched the organ of the Society, Madroño, which he edited continuously through 1934. Much earlier, with the aid of E. L. Greene, he had founded and edited the journal Erythea.

The botanical writings of Jepson are both extensive and profound, and they have exerted a lasting influence upon our knowledge of the botany of California. The present account attempts to evaluate Jepson's lifework, as made known by these contributions, on the historical background.[1] A bibliography of authors who have named flowering plants occurring in the wild in California now includes well over 900 names! Where does Jepson stand among these?

Three stages can be recognized in the study of the California flora: (1) its study by Europeans; (2) by Americans along the eastern seaboard; and (3) by Californians. The first stage dates back to the late eighteenth century, when European explorers began to collect the objects of natural history that they found on these shores. By the early nineteenth century people in England had become greatly interested in horticulture, and expeditions were sent out to the four corners of the earth in search of plants to enrich British gardens. Bent on this purpose and showing amazing activity, David Douglas alone, Scotch collector for the Horticultural Society of London, now the Royal Horticultural Society, in his single season in California provided the material from which some 300 species were to be described.

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[1] For sketches of Jepson, the man, giving more details of his active life, refer to (1)Herbert L. Mason in Madroño 9: 61–64, 1947; (2) Lincoln Constance in Science 105: 614, 1947; (3 & 4) Emanuel Fritz in California Forester 14: 6–8, 1947, and in Jour. Calif. Hort. Soc. 9: 23–26, 1948; (5) Marion R. Parsons in Sierra Club Bull. 32: 104–107, 1947; and (6) Joseph A. Ewan in Jour. Wash. Acad. Sci. 37: 414–416, 1947.

The second stage, led by Thomas Nuttall, began around 1830, when the botanical exploration of the West by American botanists was under way. Soon John Torrey and Asa Gray were vying with the British botanists, W. J. Hooker and George Bentham, in the volume of West American species that they were bringing to light. During much of the latter half of the century, collectors by the dozen were sending West American plants to Dr. Gray, the highest authority of the period on the flora of this region. As a culmination of this stage there appeared the monumental two volume Botany of California by W. H. Brewer and Sereno Watson, with a large section contributed by Gray (1876, 1880). This invaluable work, based principally on the large accumulations of western material that had gravitated to Harvard and also the collections of Brewer and others made in connection with the Geological Survey of California, has been the starting point for all subsequent floras that have been produced in the state.

Gradually, as the third stage in the elucidation of the California flora, the West developed its own botanical authors. The first to publish a number of native species new to science was Albert Kellogg, a San Francisco physician. His contributions appeared particularly from the 1850's to the 1870's in the Proceedings of the California Academy of Sciences, the institution of which he was a founder.

By 1880 the botanical activities of the Reverend Dr. E. L. Greene had begun. His contributions through the years were very large, but were so rarely of a monographic nature that the proportion of his specific proposals that were to be widely accepted is not to be compared with that of Gray, Watson, or Jepson. Yet, as a pioneer worker in a region outstanding for the richness of its flora, and having a keen eye for small variations, which he named, it was inevitable that Greene's name should be associated with a goodly percentage of our California species. He contributed two local floras of value: Manual of the Botany of the Region of San Francisco Bay, 1894, and Flora Franciscana, 1891–97.

The first of the major botanical works produced by Jepson, who was a student of Greene, was A Flora of Western Middle California, 1901, second edition, 1911. He usually had several manuscripts in preparation simultaneously. His work on one yielded information or suggested ideas applicable to another. About the time he finished work on this book he projected The Silva of California (1910), The Trees of California (1909, second edition, 1923), and A Flora of California, which from the first he looked upon as his greatest life's work. Jepson himself says[2] the Flora was planned in 1894. The first two parts appeared in 1909, the twelfth part in 1943. Work was actively progressing on the thirteenth part until illness interrupted, and the author's death a year later in 1946 found the Flora about three-fourths completed and published. Volume I starts on page 33, the first 32 pages being reserved for an introduction that was to have appeared upon the completion of the whole work. Its seven parts, otherwise complete, are not indexed. Volume II is complete, but the index is to families and genera only. The two completed parts of volume III are not indexed.

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[2] Flora of California 2: 7, 1936.

Jepson was thoroughly aware of these deficiencies and was almost reticent in advertising the parts of the Flora that were available. As in the case of A Manual of the Flowering Plants of California, which was also issued in parts, from 1923 to 1925, he preferred to withhold advertising of the parts as they appeared individually, because for the general user the completed work would prove more useful, and it was desirable not to deplete the stock of any one part before the entire volume could be bound. Because of these shortcomings, Jepson's Flora is definitely less convenient than his Manual, particularly for use in the field, and therefore has not received the general recognition and use that it deserves, but the quality of workmanship in the later parts is unsurpassed in any similar American work.

Jepson's major projects built progressively upon one another. As the Flora of Western Middle California built upon Brewer and Watson's Botany of California, Gray's Synoptical Flora of North America, and the works of Greene, appreciably advancing our knowledge of the plants of its area, so the Manual drew upon this work and the portions of A Flora of California then completed to become one of the finest botanical handbooks extant. Similarly, succeeding parts of the Flora mark a distinct advance over the Manual. As would be anticipated in a work that was to appear in parts over more than a third of a century, A Flora of California is uneven in treatment. The progressive improvement noted in volumes II and III as compared with volume I reflect not only the scientific growth of the author, but also the growth of botany in the West.

At a very early time Jepson had to decide whether to use the system of measurement based on the foot, inch, and line, used by the English botanists and the Harvard school, or to adopt the metric system coming into vogue on the Continent. He chose to follow the former, and, having committed his Flora to this system, was forced to continue, even though it was soon evident that the English system had been becoming obsolete from the turn of the century. By the time his Manual appeared in 1925, Jepson was originating the only major flora in America that did not follow the metric system.

This relatively minor fault, if fault it be, is nevertheless one of the few mechanical details to which exception can be taken in the works of one who put mechanical perfection very high indeed among the obligations of an author. Jepson's works are freer from typographical error than those of almost any other American botanist due to the fact that he meticulously read proof himself and left no mechanical detail to the discretion of his printer.

Jepson strove for a uniform treatment and avoided introducing chromosome numbers, genetical data, and other experimental results that, by the time the later parts of the Flora were appearing, were becoming a determinative influence in taxonomy. It is well that he stayed on wholly familiar ground, continuing to rely on those tools which he handled as an adept—accurate descriptive morphology and analysis and a keen perception for the place of the plant in its natural environment. The story that he wrote he was perhaps better prepared to write than any other person.

The inclusion in later parts of the Flora of excerpts from Jepson's very extensive field notebooks on the ecology, physiology, and morphology of many species is of great value. The reader finds much interesting and original information under such a variety of titles as: geographical note, field note, leaf variation, taxonomic note, note on relationship, biological note, etc. Jepson was not only an astute observer; he was a facile writer whose written word was forceful, clear, and often of great beauty.

His appreciation of the historical precedent and the classical style stemmed not only from his teacher, E. L. Greene, who valued these especially highly, but also from his study of the works of the greatest systematists and from a reading of the classics. He urged upon his students the desirability of becoming familiar with great works on travel and biography as a proper foundation for work in taxonomy.

Students of west coast botany are fortunate that the principal task of organizing their flora has been done by one with the sound botanical judgment of Jepson. This he did not learn from Greene, nor from other contemporaries in California, but from a devoted study of the artistry of the great British systematists of the nineteenth century. That he profited much from this study is evident from the quality of his work, which has made an impress on the writings of others.

Jepson, with an intuitive grasp of what are good species and genera, organized the scattered knowledge of the complex California flora in a remarkable way. He introduced the Englerian system of phylogeny to California, but here and there made his own appraisals of the proper positions for the families. His species concept was grounded on so sound a morphological basis that, on the whole, it has been widely accepted, and the present-day methods of the experimental gardens and the cytological laboratories usually substantiate rather than displace Jepson's judgments. Relatively few of his contemporary authors have found their work so generally acceptable.

In gauging Jepson's place in California botany, the writer was prompted by curiosity to tabulate the number of species in the state named by each author, using unchanged the data as given in Jepson's Manual, our last complete list. Despite the shortcomings of the Manual data, such as the incomplete synonymy, the resulting list is of some interest. Here are the top 15 names, including all those who have named 50 or more species in the Manual, together with the number of names contributed by each.

1.	Asa Gray	717
2.	Carolus Linnaeus	431
3.	Edward Lee Greene	365
4.	Sereno Watson	283
5.	Thomas Nuttall	266
6.	John Torrey	245
7.	George Bentham	188
8.	William J. Hooker	160
9.	Willis Linn Jepson	154
10.	David Douglas	86
11.	George Engelmann	74
12.	A. P. de Candolle	68
13.	Frederick T. Pursh	64
14.	George A. W. Arnott	58
15.	Joseph Nelson Rose	51

The only Californians among the first 15 are Greene and Jepson, and these are grouped among the classical students of the California flora. Albert Kellogg, however, with 48 species, is in sixteenth place. Other Californians among the first 50 are A. A. Heller, T. S. Brandegee, Alice Eastwood, H. M. Hall, Katherine Brandegee, and S. B. Parish, in that order.

Jepson worked in that transitional period between the time of Greene, when new species were yet to be found on almost every mountain range and valley floor, and the present, when even monographic researches uncover relatively few acceptable new species. Considering the conservative stand that he took on the matter of describing new species, it is interesting how high in the list his name is found. Jepson preferred to evaluate critically his own proposals before offering them to the world. This is one reason that his work has attained a lasting character.

The influence of Jepson does not rest wholly upon his writings. The relatively small number of graduate students that he found time to encourage came impressionably under the influence of his strong character. Their training would doubtless be considered unorthodox and irregular, but certain fundamentals about meticulous detail in observation of the plant, whether in the field or in the laboratory, and a broad appreciation for the contributions from related fields were drilled into the memory. His graduate student seminars were often his sole contact with the student. These were broadening and often dramatic experiences that challenged the imagination to reach out; they served to turn the student's attention from the local flora, with which Jepson's life would seem to be engrossed, to the far corners of the earth and to many fields untouched by Jepson's writings. The beneficial influence of this training is apparent from the sound taxonomic practices of those trained by him and, in turn, of their students.

Jepson succeeded in imparting to his public, which consisted in good part of laymen as well as of students, his deep feeling for nature. He looked upon the plant not only with the discriminating eye of the master systematist, but also with the enthusiasm and reverence of the naturalist and woodsman. Perhaps most beautifully expressed was his love for trees, so obvious in the Silva. One's love of nature is apt to govern in direct proportion one's concern for conservation, and so it was that Jepson was a founder and prominent spokesman for the Save-the-Redwoods League and a staunch advocate of forest conservation measures and such other endeavors as the Point Lobos Reserve. All in all, it has been through many channels that the works of Jepson the botanist have become known, not only to his California audience, but to the world at large.

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REVIEWS

The Evolution of Gossypium and the Differentiation of the Cultivated Cottons. By J. B. Hutchinson, R. A. Silow and S. G. Stephens. Oxford University Press. 160 pp. 10 figs. 1947. 15s.

The genus *Gossypium* is of outstanding interest not merely because of the economic importance of cotton, but in respect to the taxonomy, genetic relationships, morphology, and physiology of the plants. To botanists of the Pacific Coast the interest is enhanced by the fact that of approximately 16 truly wild species of this genus, 4 are indigenous to the shores and islands of the Gulf of California.

The scope of the admirable little book under review is indicated by its title and by the titles of the parts: Part 1, The classification of the Genus Gossypium, by Hutchinson; Part 2, The Evolution of the Species of Gossypium, by Hutchinson and Stephens; Part 3, The Differentiation of the True Cottons, by Hutchinson and Silow; and Part 4, The Significance of Gossypium in Evolutionary Studies, by Hutchinson and Stephens. It would be hard to find authors more competent to deal with these matters, all three of them having carried on original research that has advanced, substantially, our knowledge of the subject.

In treating "The Relationships of the Genus," the authors follow Edlin in transferring the tribe Hibisceae, to which *Gossypium* belongs, from the Malvaceae to the Bombacaceae, on the ground that the fruits are capsular (loculicidally dehiscent), not septicidally dehiscent into schizocarps, as in the other tribes of Malvaceae. But this distinction is not absolute because normally in *Bastardia* and occasionally in *Sphaeralcea* and other genera which no one would think of removing from the Malvaceae, the septicidal dehiscence is very imperfect. There seems to be no sharp line of demarkation between the two families and perhaps we should return to the classification of Bentham and Hooker, and regard the Bombacaceae as merely a tribe or subfamily of the Malvaceae.

In the classification of the species, the authors follow, in the main, that which was first outlined by Zaitzev, and later amplified by S. C. Harland, on the basis of cytogenetic studies. Three main groups are recognized: (1) The approximately 16 wild species, of which all that have been studied cytologically have 13 as the haploid chromosome number. None of them has true lint hairs on the seeds. These species are widely dispersed in tropical and subtropical regions of both the Eastern and Western Hemispheres, with scarcely any overlapping of their ranges. (2) The Asiatic cultivated cottons (*G. herbaceum* and *G. arboreum*), likewise with 13 haploid chromosomes, but producing lint hairs of spinnable length. (3) The American cultivated cottons (*G. hirsutum* and *G. barbadense*), with 26 haploid chromosomes and long lint hairs on the seeds. To the last group belongs *G. tomentosum,* of the Hawaiian Islands, where it is supposed to be endemic, although its affinity to the cultivated American cottons is unquestionable.

The remarkable discovery was made by Skovsted, that the American cultivated cottons possess two sets of chromosomes, 13 larger ones, similar to those of the Old World cultivated cottons, and 13 smaller ones, similar to those of American wild diploid species. This suggested that the American cultivated cottons originated as allopolyploids. Subsequent genetic investigations by Harland and Atteck, Silow, Beasley, and Stephens have strengthened the evidence of such origin, pointing to the Peruvian wild cotton, *G. Raimondii,* or a near relative, as one of the probable ancestors.

The difficulty has been to explain how contact could have been brought about between an Old World and a New World species, since the origin of the American cultivated cottons was, assuredly, pre-Columbian. Harland assumed a southern trans-Pacific land bridge in Cretaceous or early Tertiary times, but apparently insuperable objections to this hypothesis are given in the book under review (pp. 75, 76). The authors (pp. 77–80) prefer the assumption that seeds of an Old World cotton were brought to America and planted there by prehistoric voyagers across the Pacific. Such an explanation cannot be dismissed as impossible, but a third, and in the reviewer's opinion a more plausible hypothesis, has been advanced recently by Stebbins (Ecol. Mon. 17: 155), who points out the significance, in relation to this problem, of the mingling of Asiatic and New World floral elements in Eocene deposits of North America. Although no traces of *Gossypium* have been found, as yet, in such deposits, it is an attractive possibility that a cotton, related to the Old World cultivated diploid species, might have existed in the Western Hemisphere during the Tertiary, in contact with an American diploid species, and that hybridization between them might have produced the ancestors of the American tetraploid cultivated cottons.—THOMAS H. KEARNEY, California Academy of Sciences, San Francisco.

The New World Cypresses. Part I. Taxonomic and Distributional Studies of the New World Cypresses, by CARL B. WOLF. *Part II. Diseases of Cypresses,* by WILLIS W. WAGENER. *Part III.*

Horticultural Studies and Experiments on the New World Cypresses, by Carl B. Wolf. Pp. xvi + 444. Appearing as volume I of El Aliso, A Series of Papers on the Native Plants of California, published by the Rancho Santa Ana Botanic Garden, Anaheim, California. 1948. $4.00 buckram, $3.55 paper bound.

The new publication El Aliso gets off to an auspicious beginning with this excellent treatise on the New World cypresses as its first volume. As explained in the forword written by the editor, Philip A. Munz, this journal is founded to care for the botanical and horticultural papers issuing from the Rancho Santa Ana Botanic Garden and will appear at irregular intervals. The name, El Aliso, was that used by the Spanish Californians for the native sycamore.

The genus *Cupressus* has received excellent attention at the hands of Wolf and Wagener. These scientists were well qualified for their task, each with nearly 20 years' experience with cypresses behind them before writing their contributions. Dr. Wolf, until recently Botanist at the Garden, has contributed Part I, a 250-page detailed taxonomic and distributional account of the species, and Part III, 115 pages on their horticulture. Dr. Wagener, of the Division of Forest Pathology of the United States Department of Agriculture, has written Part II, of 68 pages, on the diseases of the American species. Their work was mutually cooperative from the year 1934. The first cypresses were planted at the Rancho Santa Ana Botanic Garden in the year of its founding, 1927, and a thorough investigation of this genus of trees soon became the most ambitious single project undertaken by the Garden.

Eleven of the sixteen entities recognized are native only in California, and Dr. Wolf has collected and grown material from three-fourths of the known groves in the state. In Part I fifteen species are recognized as native in the New World, one of which, *C. Bakeri,* is composed of two subspecies. Two species are new: *C. Abramsiana,* known definitely but from two stations on Ben Lomond, Santa Cruz Mountains, and *C. Stephensonii,* known from a scattered stand about one mile in extent along the upper limits of King Creek, Cuyamaca Peak, San Diego County, both of which must be counted among the rarest tree species in California. Also new is *C. Bakeri* subsp. *Matthewsii* of the Siskiyou Mountains of Josephine County, Oregon, and Siskiyou County, California.

In the systematic section the order of treatment appears to be rather arbitrary. One feels that Wolf uncovered very few clear patterns of relationship within the genus, but that had the scattered discussions been drawn together in one strong subchapter on relationship the picture would have been clearer to the reader, and one or two improvements in the order of treatment would have been obvious.

The species concept employed is easily defended from the point of view of the horticulturist, to whom differences in habit, herbage color, etc., are of importance, although Wolf grants that some of the separations are difficult to make from herbarium material. Similar difficulties confront us in the classification of the pines, oaks, and many other arboreal genera. Perhaps in woody plants of horticultural or economic importance we are being most expedient in recognizing differences of a sort that are passed over more lightly in the herbaceous species. Wolf is aware of the problem and more than once discusses what his more conservative treatment of the New World cypresses could have been—7 species instead of 15. From the relatively minor nature of the morphological differences between the species, one speculates as to whethter there might prove to be even fewer biologically distinct entities, but no crossing experiments have been attempted. Wolf appearently has seen no tree in the wild that he considers to be an interspecific hybrid.

In Part II Dr. Wagener gives a clear account of the diseases found in American cypresses, the most serious of which is the Coryneum canker, known in California only since 1915 but now spread through and having almost eliminated most of the planted Monterey cypresses in the state. Fortunately, protective measures have been effective in keeping it out of the native groves of the native groves of the species. Susceptibility to the disease was tested in two plots established at Stanford University, and the coastal species were found to be most susceptible, and the inland the most resistant.

In Part III Wolf describes the growing of cypresses and gives the experience obtained in numerous test plots. An evaluation of the horticultural possibilities of the species is then presented.

Good stock, presswork, and binding have combined to make an attractive book. A candid review, however, must touch upon the weak organization and lay-out of the material. For example, the book is liberally illustrated, a number of the 80 halftones being composed of 2 or 3 photographs, but it is unfortunate that 66 of the 80 have their legends on the opposing, or some other, page. Judicious trimming of the photographs would have improved many of them and allowed this number to be reduced to an approximate 10. In part I the narrative style results in long descriptions and citations of localities and collections. One wades through much extraneous matter to get at any one class of information, such as the ecology of cypress. The synonomy is given twice, in an effort to draw like materials together, but it is disturbing to find that the two references do not always agree, as in the authority for the combination *C. Goveniana* var. *Sargentii.* Headings are not graded in descending order of importance, nor do those in the text always parallel those in the table of contents, and the dual legends employed in the last eleven tables should preferably have been avoided. Finally, in so comprehensive a treatment of a genus like *Cupressus,* with species distributed in groves so admirably suited for the purpose, the lack of distribution maps is keenly felt. All of these detractions are minor, however, as weighed against the wealth of material to be found in this volume, and the thanks of all persons interested in cypress are due the authors.

We can now set this cooperative treatment of a native tree important to horticulture beside a similarly conceived book on another horticultural subject, *Ceanothus,* put out in 1942 by the Santa Barbara Botanic Garden. Our California botanic gardens appear to be producing just the type of work for which they are better fitted than anyone else. May the list of their contributions become a long one!—David D. Keck, Carnegie Institution of Washington, Stanford, California.

NOTES AND NEWS

Elymus aristatus in California. What is apparently the first definite California station for *Elymus aristatus* Merr., a species occurring mainly from Washington and Montana south to Nevada and California, was established by the writer in 1941 when this species was collected in Mono County, twenty miles northwest of Bridgeport (*Gould 1325*). According to Mrs. Agnes Chase of the United States National Museum this grass was known previously in the state only from two Bolander collections whose locations were stated merely as "California." At the site of the Bridgeport collection *E. aristatus* was observed growing with *E. cinereus* Scribn. & Merr. on a dry, open hillside in an *Artemisia tridentata* association. Both species of *Elymus* had a strongly developed bunch-grass habit with culms in large clumps. *Elymus aristatus,* however, differed conspicuously from the more familiar *E. cinereus* in its long awns and non-glaucous culms and leaves. The paucity of California records of *E. aristatus* is probably not a true index to the abundance or range of the species in the state. Further collections from the foothills of the central and southern Sierra Nevada are certainly to be looked for. The writer is indebted to Mrs. Chase for information concerning the Bolander collections and for confirming the identity of his own specimens. —Frank W. Gould, Department of Botany, University of Arizona, Tucson, Arizona.